The Palaeobotanist, **28-29**: 81-85, 1981.

PHLOEM HISTOLOGY OF A LOWER PENNSYLVANIAN *PSARONIUS*

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This manuscript is dedicated to Dr K. R. Surange in the year of his retirement for his numerous contributions to the study of fossil plants.

ABSTRACT

Phloem anatomy of a *Psaronius* species is described based on Lower Pennsylvanian coal ball specimens. The phloem tissue completely surrounds the C-shaped xylem strands and is separated from it by a 3-cell wide parenchymatous sheath. The phloem zone consists of a central band of large diameter sieve elements that are bordered by zones of phloem parenchyma on each side. The abaxial phloem tissue is more extensive than the adaxial phloem and contains very small diameter cells which may represent protophloem. The phloem anatomy of *Psaronius* is compared with that of extant marattialeans.

Key-words — Histology, Phloem, *Psaronius*, Marattiales, Lower Pennsylvania.

सारांश

अधर पेन्सिलवेनियन सैरोनियस की पोषवाह औतिकी – ऍडिथ एल० स्मूट एवं टॉमस एन० टेलर

अधर पेन्सिलवेनियन कोल-बॉल के नमूनों पर आधारित एक सैरोनियस जाति की पोषवाह-शारीर का वर्णन किया गया है। पोषवाह ऊतक सी० आकार के दारु संपूल को चारों ओर से घेरे रहता है तथा इससे तीन कोशिका चौड़ी मृदूतक आच्छद से पृथक्कृत रहता है। पोषवाह मंडल एक केन्द्रीय पट्टी में स्थित बड़े व्यास वाले चालनी तत्वों से बना है जो दोनों ओर पोषवाह मृदूतक मंडलों से सीमित हैं। अपाक्ष पोषवाह ऊतक अभ्यक्ष पोषवाह की अपेक्षा अधिक विस्तृत है तथा इसमें बहुत छोटी व्यास वाली कोशिकायें पाई जाती हैं जो कि शायद आदि-पोषवाह का निरूपण करती हों। सैरोनियस की पोषवाह-शारीर की तुलना वर्तमान मैरेट्येलियनों से की गई है।

PHLOEM constitutes one of the tissue systems in fossil plants that historically has been very poorly understood. Within recent years there has been increased investigation of the anatomy of this tissue in several major groups of Carboniferous plants. These include members of the Lycophyta (*Lepidodendron*, Eggert & Kanemoto, 1977), Sphenophyta (*Sphenophyllum*, Eggert & Gaunt, 1973; *Astromyelon*, Wilson & Eggert, 1974), Pteridospermophyta (*Calamopitys*, Galtier & Hébant, 1973) and Pteridophyta (*Etapteris*, Smoot & Taylor, 1978; Smoot, 1979; *Botryopteris*, Smoot, 1979).

While an understanding of the phloem anatomy of these plants is important in suggesting basic evolutionary trends in phloem structure, none of these taxa can be related to extant orders so that a direct comparison between living and fossil forms is not possible. One group of vascular plants that has an extensive fossil record and includes a number of extant genera is the Marattiales. The fossil members of this order are known as a number of form genera associated with the structurally preserved tree fern *Psaronius*. Among the extant members of this order are 6 or 7 genera and approximately 100 species, all of which are tropical and confined to narrow geographic regions.

The discovery of several stems of *Psaronius* sp. with exceptionally well preserved phloem from the Lewis Creek coal ball locality (Lower Pennsylvanian) provides a unique opportunity to examine the phloem anatomy of a Carboniferous member of the Marattiales and offers a basis of comparison with extant forms,

The specimens used in this study consist of stem and petiole fragments preserved in calcium carbonate. Surfaces were prepared for examination in transmitted light using the well-known cellulose acetate peel technique. Stem and petiole fragments were prepared for the scanning electron microscope according to the technique outlined earlier (Smoot, 1979).

DESCRIPTION

This study is based on 3 specimens, the largest of which is flattened and measures 34 cm long and 3·5×12 cm in diameter. None of the specimens is complete; the best preserved axis consists of an external ring of sclerenchyma surrounding a number of scattered vascular strands together with other fragmented plant parts. The parenchymatous ground tissue is typically not preserved. Attached to these stems are axes containing C-shaped vascular strands. In some instances these axes no doubt represent petiole bases since they occur to the outside of the delimiting zone of sclerenchyma. In other cases the vascular strands occur to the inside of the sclerenchyma sheath and therefore may represent either departing leaf traces or segments of the stem. Associated with some of the axes is a narrow band of adventitious roots that are embedded in a common parenchymatous zone.

Despite the relatively poor preservation of the stems, many of these C-shaped vascular strands possess a well-preserved phloem zone that surrounds the xylem. In addition, a few cortical tissues are present external to the phloem.

Figure 1 illustrates a transverse section of a portion of one of these strands and exhibits the continuity of vascular tissues.

The central portion of the strand consists of a bar of metaxylem tracheids up to three cells in width. Individual cells measure up to 3 mm long and exhibit scalariform pitting on the walls. Protoxylem tracheids occur scattered along the inside (adaxial) margin of the vascular segment and are typically less than 36 μm in diameter. Protoxylem pitting appears to be helical to scalariform, however, most of the elements appear badly crushed in longitudinal section. Many of the metaxylem tracheids are characterized by numerous tylosis (Pl. 1, fig. 5).

Surrounding the xylem segment is a uniform zone of thin-walled parenchyma up to three cells in thickness — the so-called xylem sheath (Pl. 1, fig. 2). These cells measure approximately 50 μm in diameter, and at some levels grade imperceptibly into the phloem tissue. Typically the two zones can be distinguished by the slightly thicker walls and smaller diameter of the phloem parenchyma cells (Pl. 1, fig. 2).

The phloem of this *Psaronius* is a relatively complex tissue. The C-shaped bundles are amphiphloic, however, the components of the phloem tissue differ slightly on the inner and outer faces of the vascular segment. On the inner surface of the segment (adaxial), immediately adjacent to the parenchyma sheath is a region of phloem parenchyma, a single cell in thickness. At some levels this zone is absent. Outside of the phloem parenchyma on this surface is a discontinuous row of elongate sieve elements that may reach lengths of 120 μm. The end walls of the sieve elements are oblique and rounded (Pl. 1, figs 3, 6), and the individual elements are connected end to end to form a longitudinal series of cells that is continuous (Pl. 1, fig. 5). Longer sieve elements are characteristically subdivided by thin cross walls that are normally oriented perpendicular to the long axis of the cell (Pl. 1, fig. 6). Slightly oblique walls have also been observed. These internal cell walls often appear translucent, and their thickness compared to that of other cell walls may indicate the absence of secondary wall material.

The adaxial sieve elements usually exhibit slightly thinner walls than do those in the abaxial phloem zone. External to the zone of sieve elements is a narrow layer of phloem parenchyma that borders directly on the inner cortex (Pl. 1, fig. 2).

The phloem on the abaxial surface of the xylem trace is organized in a similar way to that of the adaxial surface except that the individual zones within the tissue are more extensive. The phloem parenchyma external to the sheath is 3-4 cells wide (Pl. 1, fig. 5), the sieve elements form a fairly continuous layer (Pl. 1, fig. 2), and the outer phloem parenchyma may be up to 4 cells wide. Between the abaxial sheath parenchyma and the phloem parenchyma

is a discontinuous zone of small diameter cells (8 μm) that can be distinguished from the parenchyma cells on the basis of their slightly thicker walls. These cells appear to be evenly distributed across the abaxial phloem zone and may represent protophloem. Although a few small diameter (16 μm) cells are present in the adaxial phloem, the larger size of these cells and their scattered arrangement suggests that they probably do not represent protophloem.

Histologically the cortex consists of three zones. Immediately adjacent to the phloem is a narrow zone (3-5 cells) of thin-walled parenchyma which is often poorly preserved (Pl. 1, fig. 1). The middle cortex consists of slightly larger cells with appreciably thicker walls, and vertically elongate mucilage ducts, each lined with a ring of partially degraded parenchyma. In transverse section these ducts are situated in a row on either side of the vascular segments (Pl. 1, fig. 1). None have been observed scattered throughout the cortex as in some species of *Psaronius*, however, the distribution of these ducts may be dependent upon the ontogenetic level of the stem and may have little systematic significance. The outermost cortical zone that is preserved consists of a narrow band of sclerenchyma cells that average 30 μm in diameter.

DISCUSSION

Perhaps the most interesting aspect of this study is the striking similarity of phloem structure that exists between the fossil taxon *Psaronius* and living marattiaceous genera like *Marattia*. Since the phloem of living marattiaceous ferns has not been extensively studied using modern techniques, comparisons between fossil and extant members are possible only at a basic anatomical level.

The distribution of tissues includes amphiphloic vascular segments in both genera. *Marattia*, like *Psaronius*, has a phloem zone that consists of a central band of sieve elements that is surrounded by phloem parenchyma. Plate 1, figure 4 illustrates a portion of a vascular segment in *Marattia*. The sieve elements are visible as slightly larger diameter cells within the phloem zone. In addition, the abaxial phloem appears to be more extensive than the phloem of the adaxial region. Shove (1900) has suggested that the greater thickness of the abaxial phloem zone in *Angiopteris* may be in part due to the presence of protophloem on that surface. This author also noted that the sieve elements in the external phloem (abaxial) may be slightly larger and more thick-walled than those of the internal zone.

The topographic position of the protophloem between the xylem and the metaphloem within extant marattiaceous ferns has been noted by several authors (Shove, 1900; Brebner, 1902). This position, which results in centrifugal development of the phloem, appears to be unique among the ferns, and may be unique among seed plants as well (Esau, 1969). It is interesting that this developmental sequence appears to be consistent in the fossil forms as well, assuming that smaller cells that have been identified in *Psaronius* are indeed protophloem elements. Since this can be determined with certainty only in a developmental framework the cells indicated here as being protophloem elements are identified based only on their morphology. Studies currently in progress are designed to more fully characterize the phloem of *Psaronius* including the characterization of sieve element wall structure and aspects of fossil marattiaceous phloem development.

ACKNOWLEDGEMENTS

This study was partially supported by funds from the National Science Foundation (DEB 77-02239).

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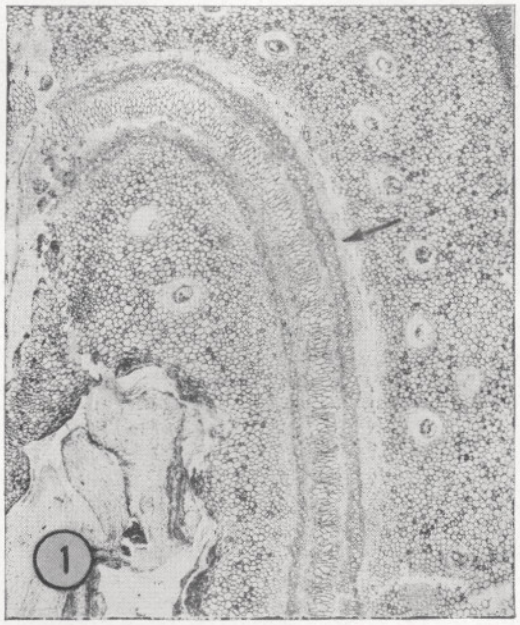
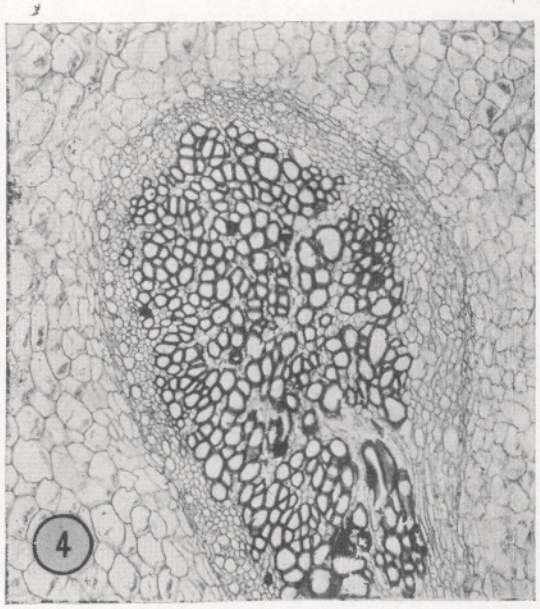
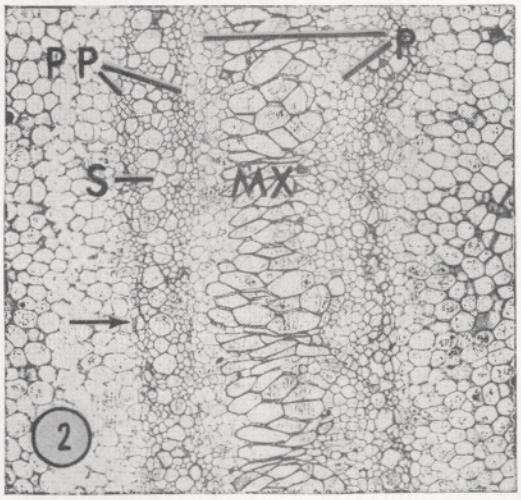
EXPLANATION OF PLATES

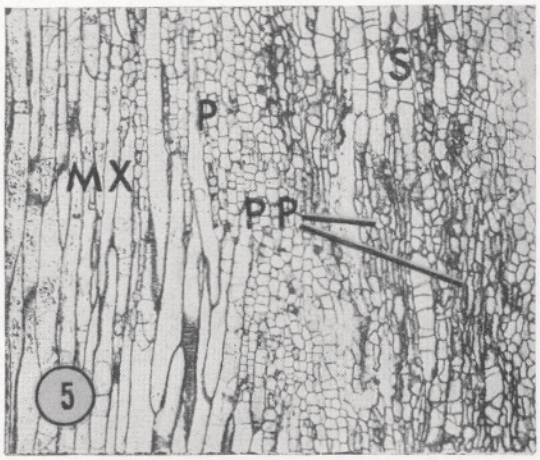
PLATE 1

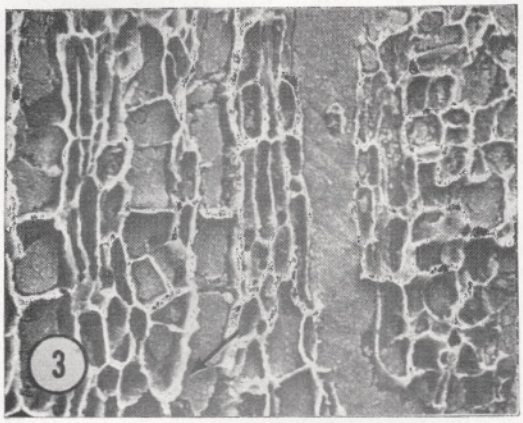
1. Transverse section of a portion of a *Psaronius* axis showing cortical mucilage ducts and vascular segment. Arrow indicates abaxial surface of vascular segment. C.B. 7700 K top, no. 7.× 6·5.
2. Transverse section of *Psaronius* vascular segment showing disposition of tissues. Arrow indicates abaxial surface. (**P**=Parenchyma of xylem sheath, **PP**=phloem parenchyma, **MX**=metaxylem, **S**= sieve elements) C.B. 7700 K top, no. 7.× 27.
3. Surface etched section of *Psaronius* vascular segment illustrating disposition of phloem elements. Arrow indicates rounded end of sieve element. Smaller diameter phloem parenchyma cells are visible surrounding the central sieve elements, and part of the sheath parenchyma appears at the far right. C.B. 7700 A, Stub no. 1.× 100.
4. Transverse section of part of a vascular segment in a *Marattia* rhizome showing central metaxylem tracheids surrounded by phloem zone, which consists of small parenchyma cells and larger diameter sieve elements.× 40.
5. Oblique longitudinal section of *Psaronius* vascular tissue indicating position of component cell types. Legend same as that in fig. 2. C.B. 7700 D_1 side no. 20.× 27.
6. Longitudinal section of *Psaronius* vascular segment in region of sieve elements. Note rounded end walls (arrow) and thinner transverse internal cell walls. C.B 7700 D_1 side no. 20.× 110.











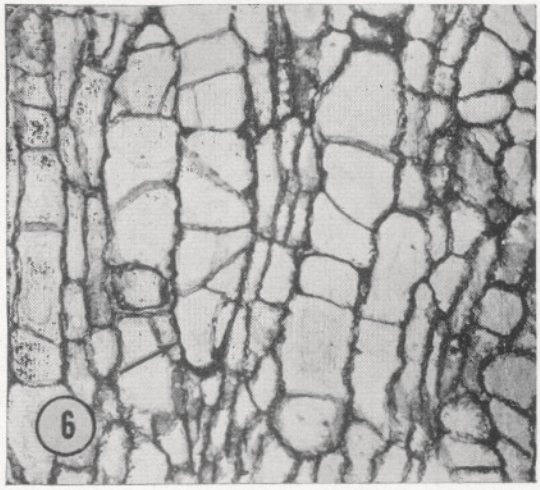


PLATE 1